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COVER

Pinguicula macroceras. Photo taken by Jurg Steiger in March, 1979.

The co-editors of CPN would like everyone to pay particular attention to the following policies regarding your dues to the ICPS.

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Views expressed in this publication are those of the authors, not necessarily the editorial staff.

Copy deadline for the Sept. issue is Aug. 1, 1982.

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News and Views

ALLEN LOWRIE (6 Glenn Place, Duncraig 6023, Western Australia) has just returned from Borneo and reports that his *Nepenthes* cuttings arrived safely using the following method: The cuttings were placed in plastic bags with only enough water to mist the sides of the bags after they had been sealed 20 minutes.

BILL NETHERBY (P.O. Box 1, Mt. Herman, CA 95041) recently persuaded the garden editor of the Santa Cruz Sentinel to do a spread on CP. The articles by Keith Muraoka appeared in two installments and generally described the habits of CP that we know so well. We thank Bill for calling attention to CP and to CPN where interested plant growers can expand their interests.

TONY REA announces that the San Francisco Flower Show will take place August 27-29 at the Hall of Flowers in Golden Gate Park. Bay Area CPN members will be sent an application. See CPN 10(4), 101 (1981) for details.

Our intrepid correspondent DALE SPEIRS of Calgary, Alberta sent an interesting article from an 1875 issue of Botanical Gazette (1:66-67). It is actually a review of other current periodicals in which is mentioned an article in the October American Naturalist by Prof. W. J. Beal entitled *Carnivorous Plants*. The usual genera are listed along with *Silene* spp. which often crops up in the older literature in this respect. However, another genus we had not before considered was also discussed in some detail, this being the species *Martynia proboscidea*. As often happens over time, the genus has now been changed to *Proboscidea* in the family Martyniaceae, two rather common and widespread species being *P. louisianica* and *P. parviflora* in North America. The genus is most recognized for its peculiar fruit from which the common names "unicorn plant" and "devil's claws" are derived. The fruits are often pickled as food. Prof. Beal apparently felt that the densely glandular character of vegetative portions of the plants (similar to *Silene* in this respect) was an indication that it was carnivorous, and he went so far as to

(Continued on page 45.)

SEED BANK*

Patrick Dwyer (St. Michael's Episcopal Church,
49 Killean Park, Albany, NY 12205)

$.75 per packet

Byblis liniflora (2), *Cephalotus follicularis* (1), *Darlingtonia californica* (3), *Dionaea muscipula, D. aliciae* (9), *D. auriculata* (8), *D. arcturi* (3), *D. binata* (1), *D. binata multifida* (2), *D. brevifolia* (2), *D. burkeana* (3), *D. burmannii*(8), *D. capensis, D. capensis* (narrow), *D. capillaris* (2), *D. filiformis filiformis* (3), *D. indica* (3), *D. intermedia, D. linearis* (1), *D. macrophylla* (2), *D. montana* (13), *D. natalensis* (1), *D. peltata* (6), *D. planchonii* (3), *D. pygmaea* (1), *D. rotundifolia, D. rotundifolia* (Oregon) (2), *D. spathulata* (7), *D. spath.* (Kansai), *D. spath.* (white fl.) (2), *D. stenopetala* (1), *D. whittakeri* (3), *Nepenthes ampullaria* (6), *N. gracilis* (10), *N. khasiana, N.mirabilis* (13), *N. rafflesiana* (12), *Pinguicula primuliflora* (1), *P. vulgaris, Sarracenia flava, S. leucophylla, S. minor* (14), *S. purpurea heterophylla* (6), *S. purpurea purpurea, S. purpurea venosa* (10), *S. rubra* (4), *S. flava* × *oreo* (1), *S. leuco* × *alata* (1), *S. psitt.* × *minor* (4), *S. sp. mix* (3), *Utricularia racemosa* (1), *U. subulata* (1).

*For instructions on how to send or order seed, see CPN March 1982, page 4.

Continued from March 1982

From

SINNESORGANE IM PFLANZENREICH

by Gottlieb Haberlandt

Insectivores: *Dionaea muscipula*

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Upon treatment with zinc chloride-iodine solution[3], these underlying cell wall layers exhibit only a light yellowish-grey coloration, while the epidermal outer walls of the leaf blades up to the cuticle immediately turn an even shade of blue. There can scarcely be a doubt that, just as in the case of *Aldrovanda*, the differing chemical behavioral of the outer walls of the hinge cells correlates with their flexibility and elasticity.

The radial longitudinal walls (side walls) of the hinge cells are considerably thickened. This is easily observed on crosswise microtome sections (Plate VII, Fig 2) and tangential longitudinal sections through the hinge (Fig. 5). On tangential longitudinal sections one also sees that the upper and lower peripheral portions of the longitudinal walls are thinner and, as a result, the cell lumina are enlarged at these points. The longitudinal walls turn blue and swell greatly when treated with zinc chloride-iodine[3]. Even without further treatment, after the protoplasts have been fixed with chrome-osmium acetic acid[8], a delicate cross-striation of the somewhat swollen longitudinal walls is observed, resulting from the presence of more numerous plasmodesmata between the adjoining hinge cells (Plate VII, Fig 3)[9]. The sloping lateral walls, which border on the hinge cells above and below, are just as thin as the radial walls of the adjacent epidermal cells, corresponding to them.

The inner walls of the hinge cells are again quite thick (Plate VII, Fig. 1); but the thickening does not usually extend all the way to the upper and lower transverse edge of the inner wall. These walls also are traversed by plasmodesmata[9], such that the protoplasts of the hinge- or sensory cells are connected not only with one another, but also with the protoplasts of the central cell bundle.

This cell bundle, surrounded by 15-16 hinge cells in the form of a ring, consists of longitudinally stretched cells with perpendicular, or only slightly slanted, transverse walls (Plate VI, Fig 10). The bundle is, as a rule, two cell layers high, and on median lengthwise sections, three cell layers wide. In the case of an exceptionally weakly constructed bristle, I found a single longitudinally stretched cell in place of the entire bundle. The content of these cells includes a living plasmatic body with an ellipsoidal nucleus. The nature of their walls is peculiar. They are more or less thickened, and, with relatively weak magnification, appear as though they are covered with rounded pits. (This corrects the mistaken description of these cell walls in the first edition of this book, p. 113.) Renewed investigation, however, explained this appearance. Many strongly refractive granules, or sinuate platelets, are embedded in the middle lamellae in a single layer. To judge by their reactions, they consist of a cutose substance[10]. On thin microtome sections (5-10 µm thick) one sees very clearly, with sufficiently strong magnification, that the rows of granules are covered on both sides by smooth cellulose lamellae, which correspond to the layers of secondary thickening (Plate VII, Figs 1, 2). Such cutin granules also occur in the partition walls between the hinge cells and the central cells. It is worth noting that, except for the longitudinal walls, only the transverse walls inside the hinge cells exhibit this construction. The upper- and lowermost transverse walls, through which the cell bundle borders on the adjacent tissue, consist of relatively pure cellulose and have no granules. On the whole, those characteristic wall properties are not so much determined by the cell boundaries, as much more by the upper and lower boundaries of the hinge. Here, the height of the hinge is equal to the height (or length) of the inner walls of the

epidermal hinge cells. The walls of the cells existing within these boundaries and the cell parts exhibit the qualities just described. Therefore, it may be concluded that these characteristic wall properties are connected with the function of the hinge. The importance of the deposition of numerous cutose granules in the cellulose wall is a complete mystery.

In the first edition of this book, I considered the central cell bundle in question to be the mechanical tissue of the entire hinge, and compared it, as far as its function is concerned, with the central body of leaf pulvini. This conception was based on the incorrect assumption that the radial longitudinal walls of the hinge cells were thin and delicate, such that the presence of a central mechanical cell bundle would be conceivable. Now, however, the laminar hinge cells in general appear to be so thick-walled that a special mechanical cell bundle in the middle of the hinge probably is superfluous. Since there are plasmodesmata between the hinge cells and the central cell bundle, the most important function of the bundle must be to transmit to the pedestal, or lamina, the state of excitation caused by deformation of the hinge cells[11].

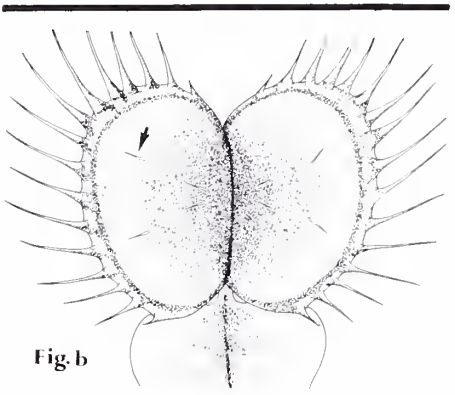

Fig. b

Fig. b. A large leaf of *Dionaea* in its spring form. An arrow points to one of the bristles (trigger hairs) on the surface of the leaf. This particular leaf has eight bristles as many larger leaves do. Leaves with six bristles would have one bristle, in place of the centrally located pairs of bristles, located on each side of the blade exactly between the pairs of bristles nearest the midvein. Haberlandt's Fig. 10 in Plate VI is a longitudinal section through the base of one of these bristles.

4. The undermost part of the tactile bristle is formed from a cylindrical pedestal which is approximately as high as it is wide. It consists of thin-walled, plasma-rich parenchymatous cells, which are occasionally faintly collenchymatous, and are surrounded by an epidermis having rather elongated cells. It is worth noting that only the innermost layers of the moderately thickened outer walls of these epidermal cells are stained blue by zinc chloride-iodine, while the outer layers take on the same yellowish-gray color as the outer walls of the hinge cells, without being cuticularized. This indicates that when the bristle is more severely bent, both the actual hinge and the pedestal are slightly bent. In agreement with this, the pedestal is not broadened at its base. Indeed, it is inclined to be thinner here than it is further above. (See Haberlandt, 1896, Fig. 207; Goebel's illustration is incorrect in this issue.) By more severe bending of a bristle under a microscope, one can readily observe that, in fact, the pedestal is also bent (Haberlandt, 1896, Fig. 208). And indeed this bending is provided for in the structure of the pedestal. When the bristle is severely bent, as it is particularly after the leaf halves close, its function evidently is to prevent a too great, possibly permanently damaging deformation of the hinge. However, with weaker impulses this is probably the only place bending will occur. The strongest bending will undoubtedly occur in the hinge zone characterized by the ring-shaped constriction.

I must now discuss briefly the nature of the deformations of the protoplasts of the hinge cells caused by their bending.

On observation of a median longitudinal section through the bristle, one sees that the hinge furrow is actually none other than a crease in the thickened outer walls (Plate VI, Fig. 10 and Plate II, Fig. 1). Each hinge cell, or sensory cell, has in its very thick outer wall a much thinner cross-striation. When the hinge is bent, the convex side is greatly stretched, while the concave side forms a fold at this point (Haberlandt, 1896, p. 208). When the convex side is stretched, the portion of the plasma membrane adjoining the thin wall striation is subjected to extreme stretching, and this deformation of the protoplast, or plasma membrane, is evidently greater here than at any other place on the cell deformed by the bending. On the concave side the nature of the mech-

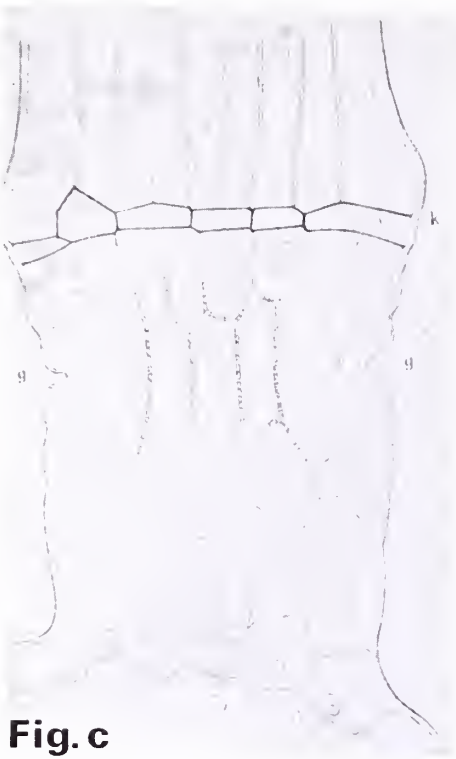

Fig. c

Fig. c. Plate IV fig. 10 from the second edition of *Sinnsorgane*. Plate VI is the same in both the first and second edition of the book except for this drawing (c.f. Plate VI Fig. 10). Note that Haberlandt changed his drawing in the second edition to indicate that all walls of the cells in the middle layer (k) are suberized instead of just the uppermost walls. Because of the much lower quality of printing of the plates in the second edition photographs of Plate VI are taken from the first edition.

anical demands placed on the plasma membrane cannot be so precisely defined. In the case of a weaker bending, it may have been subjected to a longitudinal pressure. On the other hand, with a strong bending whereby the thin portion of the outer wall folds inward, a longitudinal stretching of the plasma membrane combined with radial compression probably occurs. In any case, however, the important difference in the thickness of the outer walls of the hinge cells serves to localize the deformation on a very specific part of the plasma membrane. That the stretched plasma membrane is especially sensitive at these places, that is, under the only slightly thickened hinge striations of the outer walls, is an obvious surmise[12].

It is possible to explain more clearly the workings of the hinge furrow when the bristle is bent, if we calculate and compare with one another the bending moments of two hollow cylinders which we imagine to represent the outer walls of the hinge cells at their thickest and thinnest points. The formula for the bending moment[13] of a hollow cylinder in which the contents are neglected is: $F(r_1^2 + r_2^2)/4$. In this formula F represents the cross-sectional area, and r_1 and r_2 the radii of the hollow cylinder differing by the thickness of the wall (Schwendener, 1874, p. 23). I determined the following values for F, r_1, and r_2 on the basis of measurements of a drawing of the median longitudinal section through the hinge, carried out by means of a [camera lucida]. In the case of a hollow cylinder whose wall is formed from the thickest portion of the outer walls of the hinge cells, $F = 405$ mm^2, $r_1 = 23$ mm, and $r_2 = 20$ mm. The size of the bending moment is 93960, accordingly. In the case of a hollow cylinder whose wall thickness is the same as the thin portion of the outer walls of the hinge cells, $F = 122$ mm^2, $r_1 = 20$ mm, and $r_2 = 19$ mm. The bending moment is 23180. The actual hinge cell is therefore considerably more weakly constructed than the thickened portions of the wall adjoining on both sides. Simple observation of the dimensional relationships themselves makes this obvious. Indeed, the ratio of the bending moments is 4:1, i.e., the thickened portions of the walls of the hinge cells are approximately four times less flexible than the thin ones.

If the relationship between the structure and function of the tactile bristle presented above is correct, then it should make no difference to the resulting motor response whether the stimulation, namely the bending of the bristle, is caused by a solid object or by a fluid striking against it, for example, a jet of water. Contradicting this, Darwin (1876, pp. 263, 264) says that "drops of water or a thin, intermittent stream falling down from a certain height onto the filaments" produces no stimulation. Of course it was previously indicated by Goebel (1891, p. 202)., that raindrops usually run off the thin bristles without moving them. That will certainly be the case if the direction in which the drops are falling coincides with the lon-

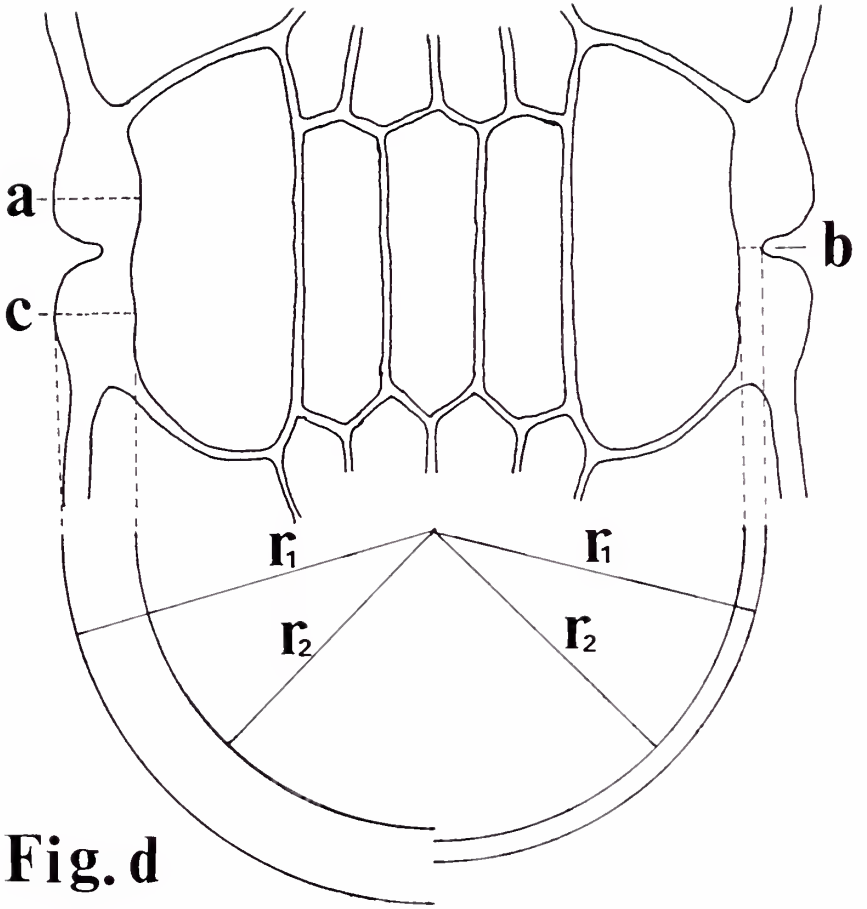

Fig. d

Fig. d. upper portion—a longitudinal section through the sensory cells of the trigger hair (c.f. Plate VI, Fig. 10). Lower right — a projection of the thickest part of the outer cuticle and cell wall illustrating one-fourth of the hollow cylinder used to compute the moment of inertia (I_c) of the thickest point. Lower left — a projection of the thinnest part of the outer cuticle and wall illustrating one-fourth of the hollow cylinder used to compute the moment of inertia (I_b) of the thinnest point. $I = F(r^2_1 + r^2_2)/4$ where F = the cross-sectional area of the projected cylinder, r_1 = the outside radius and r_2 = the inside radius.

gitudinal axis of the upright bristle, or forms an acute angle with it. If, however, a lateral jet of water is aimed at the bristles, then, as Balfour has shown, the motor response occurs immediately[14].

The tactile bristles of *Dionaea* must, according to the preceding material, be considered as very completely developed perception organs. If, on the whole, they are the most complete and most highly specialized organs of this species, then this presumes a very long period of evolution in the course of the phylogeny. This seems all the more likely since no other primitive bristles occur on the leaf which might have been the phylogenetic predecessor of the tactile bristles[15].

With regard to sensory physiology, it is highly interesting that sense perception is not exclusively limited to those highly specialized organs developed for that purpose. Various researchers, such as Darwin, Munk, Goebel and others agree that the upper side of the leaf blade is also sensitive to mechanical stimulation, albeit to a much lesser extent. Movement may also be caused by a wound.

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ENDNOTES

by Stephen E. Williams, Department of Biology
Lebanon Valley College, Annville, PA 17003

1. This very important experiment clearly shows that the "endpiece" or lever portion of the trigger hair which lies above the sensory cells of the "hinge" is not a part of the sensory system. Benolken and Jacobson (1970, J. Gen. Physiol. 56: 64-82), although they were unaware of Munk's experiments, did the same type of experiment — only in reverse. They sliced away the podium bit by bit and found that the electrical signals could be produced until they cut into the cell level of the hinge. Each of these experiments indicates that some or all of the cells at the hinge are sensory in nature, as Haberlandt states as the major thesis of this part of his work. However, it is also possible that other cells distal to the hinge cells have a sensory function as well, as has been pointed out by M. Williams and Mozingo (1971, Amer. J. Bot. 58: 538).

2. Haberlandt apparently is clouding the issue here. There is little doubt that the sensitive response is usually triggered by the hairs and that Munk and Darwin believed that to be so. The question is really whether the ability to respond is also in other parts of the leaf which, although sensitive, are more difficult to stimulate because of their structure or other factors or whether the hair is the only sensitive part of the leaf. They found other parts of the plant to be sensitive, a fact which is of some physiological interest and which Haberlandt recognizes in later parts of this chapter.

3. Zinc Chloride-iodine solution was a test for various polysaccarides which could be identified by the color they develop when treated with this solution.

4. Walls in this middle layer, which Haberlandt states are suberized, stain with Sudan black B in the same way that the walls of the endothermal layer in the *Drosera* tentacle stain (S. Williams, 1976, Proc. Amer. Phil. Soc. 120: 187-204). Lloyd (1942, *Carnivorous Plants*, p. 188) stated that he could "find very little if any suberization" in this layer. The methods used by both Lloyd and Haberlandt to detect suberization are not given. The Sudan stain, which dissolves in hydrophobic lipid structures such as cuticular wax, indicates that these walls are impermeable to water and are like the Casparian strips found in the walls of many glandular structures. There are important changes in the drawing

of this structure that were made in the second edition of *Sinnsorganne* (c.f. Fig. 10 and Fig. c).

5. The great significance of these structures is precisely due to the fact that they do not have a function. Like the leg bones of the python or our appendix they may be remnants of structures that had functions in ancestral organisms. Nearly all plant glands have an endodermis with Casparian strips of some sort. The presence of such a structure in the trigger hair of *Dionaea* is important evidence that this purely sensory structure may be derived from a secretory structure very much like the *Drosera* tentacle. The homology of the *Drosera* tentacle with the *Dionaea* and *Aldrovanda* trigger hairs is discussed in detail elsewhere (S. Williams, 1976, Proc. Am. Phil. Soc. 120: 187-204).

6. The correctness of Haberlandt's statement is easily confirmed by looking at the electron micrograph of the 1-2 μm thick cuticle of this region in Fig. 12 of M. Williams and Mozingo (1971, Amer. J. Bot. 58: 232-539).

7. Again M. Williams and Mozingo's (1971, Amer. J. Bot. 58: 232-539) observations agree with those of Haberlandt rather than those whose he is critical of. There are clearly no pores. However, the denticulations he reports are reported to be cuticular vesicles by M. Williams and Mozingo, who were observing sections of tissue less than 90 nm (0.09μm) thick in contrast to Haberlandt's 4μm thick sections. It is quite possible that denticulations which were attached to the cuticle have been cut through in a way that makes them look like vesicles in thin sections. The fact that they remain attached to the cuticle when Haberlandt hydrolized away the cellulose walls with sulfuric acid supports this interpretation (Plate VI, Fig. 11). Electron microscopic studies are best done in parallel with light microscopic work.

8. This mixture is also called Fleming's fixative. It has several variations containing different concentrations of chromic acid, osmic acid and acetic acid in water (Humason, 1967, *Animal Tissue Techniques*, p. 19).

9. These plasmodesmata were hypothesized to exist by Benolken and Jacobson (1970, J. Gen. Physiol. 56: 64-82) to explain the physiological data they observed. Haberlandt's drawings (Plate VI, Fig. 10 and Plate VII, Figs. 2, 3) clearly support their hypothesis but M. Williams and Mozingo (Amer. J. bot. 58: 538) report that these plasmodesmata do not exist. They do report large numbers of plasmodesmata connecting the sensory cells — an observation which Haberlandt failed to make. Because of the grat care with which he did his work Haberlandt's observations should not be taken lightly. However, M. Williams and Mozingo's (1971, Fig. 8) longitudinal sections show some plasmodesmata in thinner portions of the wall but not the large number reported by Haberlandt. It would be interesting to know just what Haberlandt was looking at.

10. I was unable to find Sudan black B positive walls in this part of the hair, even though it was in this region that I was expecting them. I started looking because of the analogy of these cells and the hinge cells with the sensory cells of *Aldrovanda*. If these granules are cutin they should take the Sudan stain. This observation should be repeated.

11. A thorough investigation of the distribution of plasmodesmata throughout the trigger hair and adjacent leaf blade is in order. This is the best way that the pathway over which action potentials spread can be determined. The pathway Haberlandt suggests here is questionable on the basis of a comparison of his description of the distribution of plasmodesmata with that of M. Williams and Mozingo (1971, Amer. J. Bot. 58: 532-539).

12. Haberlandt's emphasis on the cell membrane sounds very up to date. It is quite likely that the membrane is the site of reception rather than a number of other organelles mentioned in far more recent studies of the trigger hair.

13. The "bending moment" refers to the moment of inertia of the cross section of the tubular outer wall and cuticle of the hair (see Fig. d). The moment of inertia (I) together with a constant called Young's modulus (E) determines how much force it takes to bend the hair. One can determine a "stiffness factor" (S), where $S = EI$, that determines how difficult it is to bend any particular cross section through the hair. (See Thomas, *Calculus and Analytic Geometry*, Reading, Mass., pp. 550-551). Haberlandt is comparing the relative ease of bending the hair at two points along its length — that is, at the narrowest point of the hinge (point b) and at a nearby point (point a or c) where the wall and cuticle of the hair are very thick. A way to compare these is to find the ratio of the stiffness factors (S_c/S_b) at the two

points. Since $S_c/S_b = E_cI_c/E_bI_b$ it follows that $S_c/S_b = I_c/I_b$ if the Young's modulus (E) is the same at both points on the hair. The Young's modulus (E) depends on how easy the material in the wall and cuticle is to stretch. Haberlandt has assumed it is equally easy to stretch per unit cross-sectional area at both points and so he has computed $I_c/I_b = 4$. His conclusion is that it is four times as easy to bend the hair at the narrow place than at the broad places so that bending will tend to take place there. Haberlandt may have used a slide rule since his calculations are not exact, as may now quickly be ascertained with a calculator. The calculated values for I have far too many significant figures for the data anyway, so the precision is more than enough to justify the approximate 4:1 ratio of stiffness factors.

14. If the tendency of the trigger hair to require more stimuli for closure as the stimuli are delivered at less frequent intervals is added to this discussion, this would be a very accurate account of this phenomenon (c.f.s. Williams, 1980, CPN 9: 65, 75).

15. For a discussion of the evolution of this structure see S. Williams, Proc. Am. Phil. Soc. 120: 187-204.

Acknowledgments: Thanks are due to Dr. S. L. Jacobson and Dr. Y. Heslop-Harrison for reviewing the manuscript and to Mrs. Carla Lange for bibliographic help. Dr. James Scott of the Lebanon Valley College Foreign Language Department made major contributions to the translation.

Plate VII, Left Side

Dionaea muscipula

(Microtome sections)

Fig. 1. Part of a radial longitudinal section through the hinge of the tactile bristle; the sensory cell is pictured together with the protoplast (× 700).

Fig. 2. Cross section through the hinge of the tactile bristle; inside the ring of radial sensory cells is the central bundle, with cutin particles embedded in its cell walls. Fixed with alcohol, stained with paracarmine (× 660).

Fig. 3. Partition wall between two sensory cells; cross sectional view. The wall is penetrated by plasmodesmata; fixed with chrome-osmium acetic acid, stained with paracarmine (× 880).

Fig. 4. Part of a cross section through the hinge of a tactile bristle; the sensory cells touch at the upper ends, such that on the outside, the cross sections through the down-turned parts of the epidermal cells bordering above are still visible (× 660).

Fig. 5. Tangential longitudinal section (saggital section) through the sensory cells of the tactile bristle (× 700).

Fig. 6. Cross section through the upper part of the stimulator of the tactile bristle (× 480).

Plate VI, Right Side

Dionaea Muscipula

Fig. 10. Longitudinal section through the basal portion of the tactile bristle (× 440).

Fig. 11. Surface view of the hinge of a tactile bristle. The cuticle of the stimulus-sensitive cells is very finely denticulated on its inner side.

Drosophyllum lusitanicum

Fig. 14. The same, [surface view of two cells of the epidermal glandular layer] of a sessile gland.

Fig. 16. The same; [isolated protoplasts of the lateral glandular cells of a parietal tentacle, viewed from the side] the cells in question were situated more toward the apex (× approx. 900).

Fig. 17. Isolated proplasts of an apical glandular cell (× approx. 900).

Fig. 18 Surface view of some lateral glandular cells (× approx. 900).

Drosera longifolia

Fig. 19. Isolated protoplasts of two lateral glandular cells. After treatment with dilute sulfuric acid and staining with toluidine blue (× approx. 1000).

Drosera dichotoma

Fig. 21. Surface view of two lateral glandular cells of a cluster. Treated with Javelle water.

Fig. 22. Surface view of some apical glandular cells.

PLATE VII LEFT SIDE

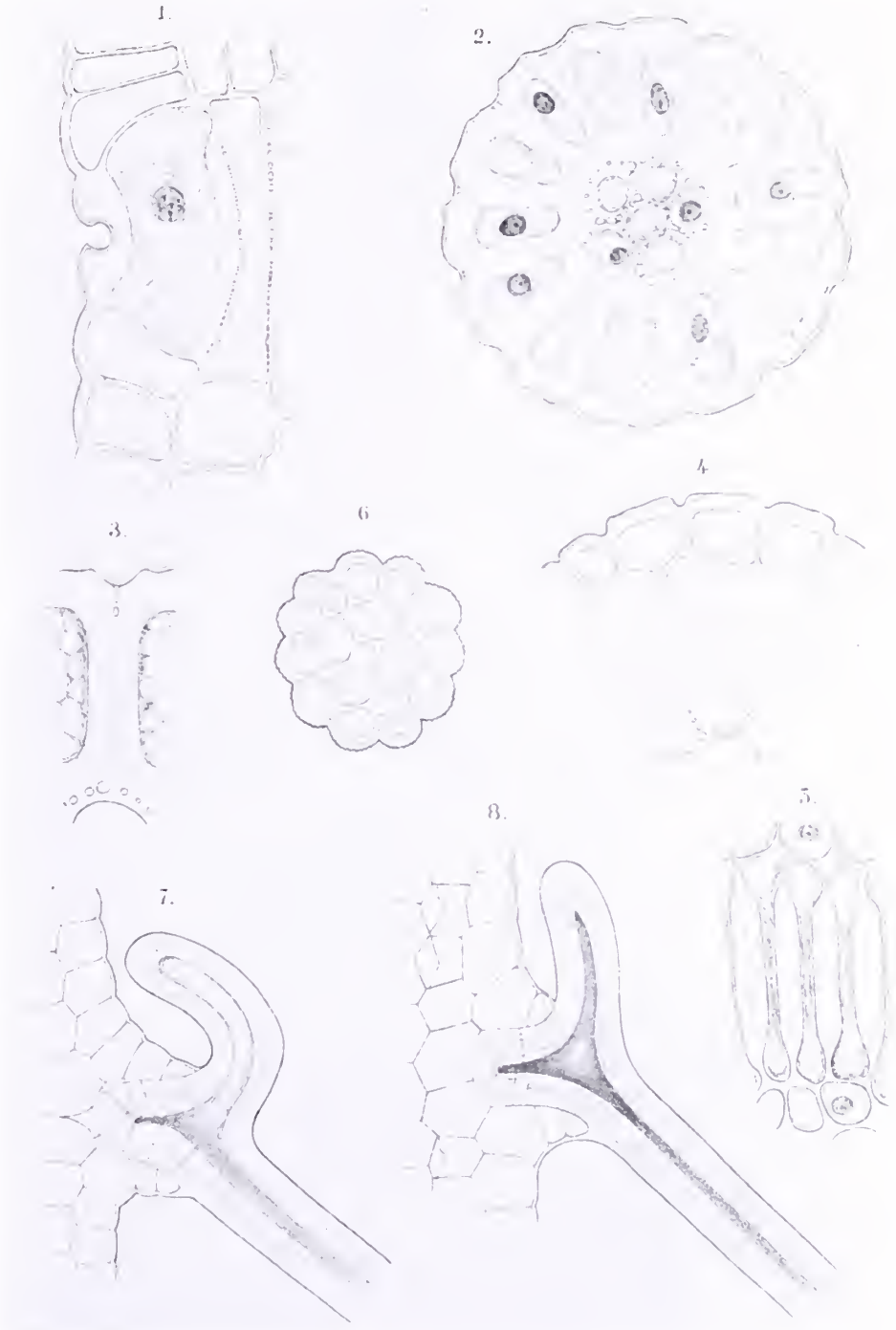
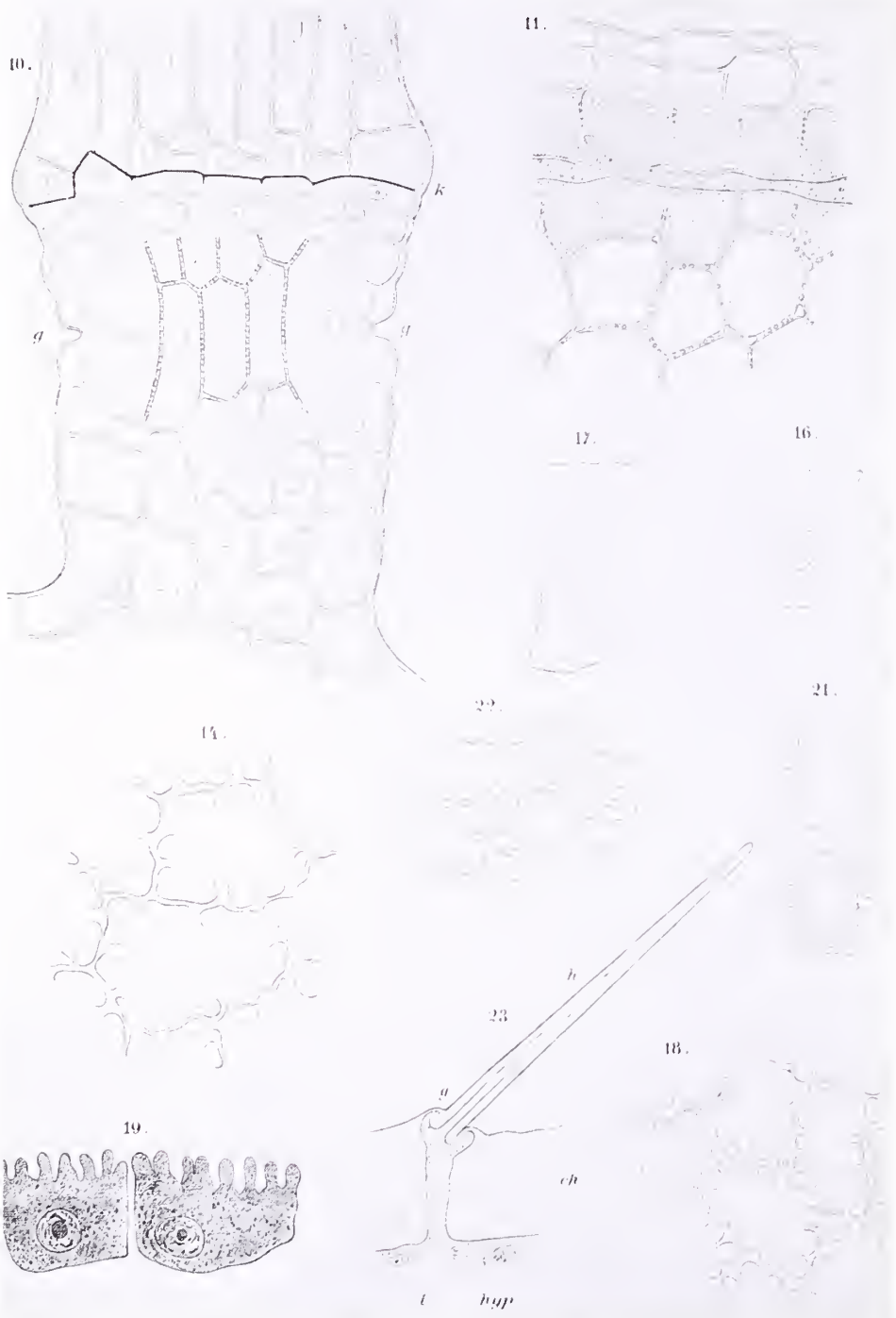


PLATE VI RIGHT SIDE



A PHOTOGRAPHIC PRIMER OF VARIANTS OF *SARRACENIA RUBRA* WALT.

by Donald E. Schnell

As was the case in the previous two editions of this primer series, text remarks must be kept brief, an especially difficult task in this very controversial species. Most regular CPN readers and students of Sarracenias are well aware of the problems of taxonomy of *Sarracenia rubra*. A selected bibliography is appended and readers are encouraged to read as many of these papers as available for details and still further important references. (Reprints of the author's papers cited are still available in limited quantities.) Throughout this discussion, the author's nomenclature will be used; it is becoming more widely and generally accepted (primarily references 5 and 8 with additional documentation in 6 and 7).

However, the other systems of nomenclature must also be studied and considered, and all papers present important concepts and insights. Wherry (9) first declared one of the S. rubras a separate species (*S. jonesii*), but was later content with subspecies status (10). Bell (1) thought the jonesii plants were but a variety and somewhat extended the putative range; he recognized no other infraspecies. McDaniel (4) felt that there were no significant taxonomic differences at all. The Cases (2, 3) however preferred to split *S. rubra* into three separate species and one subspecies. Range maps can be found in references 1, 2, 3, 4 and 5, each drawn with the author's taxonomic intentions in mind. The maps in 3, 4 and 5 are quite similar.

The numbers preceding the paragraphs below correspond to the figure numbers.

1) Flower of *S. rubra* ssp. *rubra,* quite representative of all the flowers in different subspecies, the only significant difference being in size in some populations. Note the red petals (may be pale red to maroon), reflexed sepals in older flowers. The fragrance of all sspp. is uniformly sweet or pleasant. The undersides of the petals in most plants of any ssp. is tan to tan-green in color and often has a linear red streak characteristic of the species.

2) *S. rubra* ssp. *rubra*, eastern North Carolina. The range of this ssp. is the eastern Carolinas extending inland to the sandhill counties. Within the species as a whole, there is considerable seasonal pleomorphism of developing pitchers, early spring pitchers tending to be small to etiolated with many curved forms having prominent ala. This example is quite small although flowering size, has early spring pitchers and grows in a less than ideal habitat that dries during the summer. Plants in such areas remain more juvenile.

3) *S. rubra* ssp. *rubra*, Lexington Co., SC. This example of the same ssp. as in Fig. 2 is growing in a prime habitat: an open, sunny area in sandy soil and in a large seep that is constantly wet. Note the very robust pitchers that approach other sspp. in Fig. 4 and 5 in character. One of the problems in studying the species is the wide variation due to local factors, variations that tend to be neutralized in transplant and cultivation experiments. Also, the differences between sspp. in *S. rubra* are not at all sharply discontinuous, especially when considering differences between recognized *Sarracenia* species. Many individuals of one *S. rubra* ssp. can look very much like to identical to a few individuals of another ssp. in disjunct ranges perhaps hundreds of kilometers distant.

4) *S. rubra* ssp. *jonesii* has a range limited to certain mountain counties in western NC and SC (see range maps in various references as mentioned above). Again, small ecologic variants of the ssp. or early spring pitchers have led some authors to believe that ssp. *rubra* and ssp. *jonesii* grow together, testimony to the confusion

1) Flowers of *S. rubra* ssp. *rubra*, typical of the entire species, the only significant variation being somewhat larger size in larger subspecies. Note deep red petals, recurved sepals in mature flowers. Fragrance is identically sweet or pleasant.

2) *S. rubra* ssp. *rubra*, early spring pitchers in eastern North Carolina. Note relatively smaller size of these early season pitchers in a less than ideal habitat that will dry during the summer.

3) *S. rubra* ssp. *rubra*, summer pitchers in Lexington Co., SC. Plants in this open, sunny constantly wet seep area are more robust.

4) *S. rubra* ssp. *jonesii*, mature pitchers. These are taller than ssp. *rubra* with wider tops but narrowing rapidly toward the pitcher base.

5) *S. rubra* ssp. *gulfensis* in central west Florida panhandle. While morphologically similar to Fig. 4, the pitcher top is relatively less wide, and of course the populations are widely disjunct.

6) *S. rubra* ssp. *alabamensis*. Limited (so far) to three counties just north of Montgomery, AL, the ssp. has a stockier, more robust pitcher with large hoods having undulate margins.

7) *S. rubra* ssp. *wherryi*. Morphologically similar to Fig. 6, but disjunct and in all respects uniformly smaller in proportions.

8) *S. rubra* subspecies, moderately mature pitchers in comparison photo. A) ssp. *rubra*, B) ssp. *gulfensis*, C) ssp. *jonesii*, D) ssp. *wherryi*, E) ssp. *alabamensis*. (Plants in cultivation.)

caused by seasonal and local morphologic variations in pitchers. Generally, the pitchers are quite tall in mature plants (see author's references for actual measurements) with a widely expanded pitcher mouth that narrows rapidly toward the base. The lid is well developed with a more prominent column than in ssp. *rubra,* and the upper portion of a mature, large pitcher has somewhat of a belly-like bulge when viewed from the side.

5) *S. rubra* ssp. *gulfensis*, limited to a small range in central western Florida panhandle where it is disjunct from other *S. rubra* sspp. Superficially similar in appearance to ssp. *jonesii*, the top is less wide, narrows less rapidly towards the base, and the profile bulge in the upper pitcher is absent to slight. Again, the presence of small individuals, often in less than ideal habitat has led some workers to feel that the ssp. is identical to ssp. *rubra.* An additional factor to consider in this and the other Gulf coastal sspp. is the problem of hybridization and backcrossing with other *Sarracenia* species. Considerable experience and insight may be required to sort these out in the field!

6) *S. rubra* ssp. *alabamensis* so far seems to be limited to three counties located just north of Montgomery, AL. The pitcher proportions and contour of this ssp. and the next seem relatively more different as a small group than the three preceding sspp. The pitcher is stockier in appearance although the plants grow nearly as tall as ssp. *jonesii.* The top is wider and narrows very gradually to the base in mature summer pitchers, although spring pitchers are very similar to other sspp. The very large hood is the most markedly undulated (wavey) on the margins of all. The pitcher also tends to a more pale green background color in moderate light as compared to the tan-green color of the preceding sspp., although in full light this is less apparent. A tendency to fenestrations (alveolae, light windows, etc.) is more obvious in this ssp. than others, although by no means are they clear-cut or as obvious as some other *Sarracenia* species. I feel they may seem more apparent due to the paler background color. Similar alveolae can be seen in the anthocyanin free variant of *S. rubra* ssp. *jonesii* (all yellow-green pitchers, yellow flowers) which have been found in two locations so far (5).

7) *S. rubra* ssp. *wherryi*, the last ssp. I recognize, is disjunct in extreme southern Alabama but north of Mobile Bay, particularly in Baldwin and Washington Cos. Here, the ssp. occurs with other species of *Sarracenia* (no other species have been found yet occurring with ssp. *alabamensis* above) and one must be cautious about hybrids, as in ssp. *gulfensis* mentioned in 5 above. The pitcher appears similarly proportioned to ssp. *alabamensis* but overall measurements are shorter, slightly narrower, and there is more red pigment on the average in most pitchers.

8) Finally, we come to a comparison photo of the pitchers of all five subspecies made from cultivated pitchers. The pitchers are more mature than the very pleomorphic, often non-specific spring ones, being early summer, but not as mature as full summer pitchers illustrated in previous photos. This middle stage is purposefully shown here to complete the spectrum. While it illustrates the differences between sspp. fairly clearly, it also illustrates a stage when many field observations may be made in late spring to early summer. The letter keys are given in the legend.

This has been the most difficult of the primers to present in our space limitation because here in *Sarracenia rubra* the differences felt to be present are based more on degree of a character manifestation than on a simple presence/absence factor as has been the case with most of the variants in the preceding two primers. I would reemphasize that in the case of *S. rubra* especially, one should consult at least some of the technical literature where important details, additional characters and measurements are presented along with more illustrations.

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6) SCHNELL, D. E., 1978. *Sarracenia* L. petal extract chromatography. Castanea 43:107-115.
7) SCHNELL, D. E. 1978. Systematic flower studies of *Sarracenia* L. Castanea 43:211-220.
8) SCHNELL, D. E. 1978. *Sarracenia rubra* Walter: Infraspecific nomenclatural corrections. Castanea 43:260-261.
9) WHERRY, E. T. 1929. Acidity relations of the Sarracenias. J. Wash. Acad. Sci. 19:379-390.
10) WHERRY, E. T. 1972. Notes on *Sarracenia* subspecies. Castanea 37:146-147.

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A Miscellaneous List of Places Where CPN is Cited

By L. Mellichamp

Shetler, S. G., "Carnivorous Plant Newsletter,"TAXON *27,* 478. 1978.

Slack, Adrian, Carnivorous Plants, MIT Press, 1979.

Schnell, D. E., Carnivorous Plants of the U.S. and Canada, John F. Blair, Publisher; 1976.

Schnell, D. E. & D. W. Krider, Cluster Analysis of the Genus Sarracenia L. in the Southeastern United States. Castanea *41:* 165-176. 1976.

The Kew Record of Taxonomic Literature for 1974, London. Darlingtonia and Sarracenia.

Schnell, D. E., Infraspecific variation in Sarracenia rubra Walt.: Some observations. Castanea 42: 149-170. 1977.

Schnell, D.E., A critical review of published variants of Sarracenia purpurea L. Castanea 44:47-59. 1979.

Schnell, D. E., Notes on Utricularia simulans Pilger (Lentibulariaceae) in Southern Florida. Castanea 45: 270-276. 1980.

Case, F. W. & R. B. Case, The Sarracenia rubra complex. Rhodora 78: 270-325. 1976.

N & V *(Continued from page 31.)*

calculate the prodigious numbers of small insects trapped by one large bushy plant. He placed small bits of beef on some experimental plants and "in some cases" the pieces disappeared. He further observed that trapped insects lived but a short period of time although often held by as few as one to four hairs. So, you folks living near good patches of *Proboscidea* look into this and let us know. At worst, you could end up with some interesting pickles.

DES

CULTIVATING THE ORCHID FLOWERED BUTTERWORTS

By Steve Smith Rd #1, Box 296 Kirkwood, NY 13795

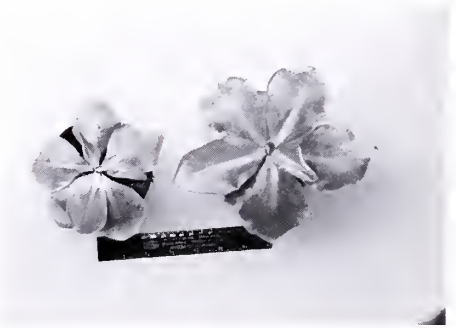
Cultivating the orchid flowered butterworts can be a very rewarding experience. The rewards include delicately shimmering leaves, beautiful flowers in the spring and sometimes leaves on plants ranging in size from 4 cm (*P. cyclosecta*) to 20 cm (*P. moranensis*). The six species of *Pinguicula* that form the *Orcheosanthus* section are: *P. colimensis, P. cyclosecta, P. gypsicola, P. macrophylla, P. moranensis* and *P. oblongiloba*. I have grown all of them with the exception of *P. oblongiloba*, which should be added by the spring of 1982. My collection also includes other species that respond well to the same cultural conditions as do the orchid flowered butterworts. These include *P. lilacina* (whose leaf margins roll down instead of up), *P. parvifolia* and *P. hirtiflora*.

These plants respond exceptionally well to cool, damp conditions that can be provided in a building cellar. Ideal temperatures for good growth will be a maximum of 26°C (78°F) during the summer and down to 10°C (50°F) during the winter dormancy period. Do not expose to freezing temperatures as you will surely lose your plants. Day and night temperatures should vary only by a few degrees for best results. The humidity is generally between 60 and 90 percent during the summer months and drops between 40 and 50 percent during the winter months, and appears to be ideal for these plants.

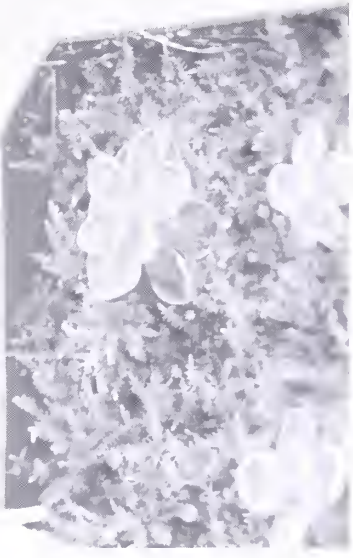
Having experimented with natural and artificial lighting, best results were obtained using the latter. I use a four-tube fluorescent fixture consisting of two Verilux Tru-bloom bulbs, one cool white bulb, and one Sylvania Gro-lux bulb. Placing the plants from 30 to 38 cm below the lights will give good size and will enhance good coloration. Distance can be increased to 61 cm or more which will result in larger plants, however, longer distances will cause loss of delicate coloration of the leaves.

I have experimented with several growing mediums, and to date the best results have been obtained using chopped sphagnum moss. Plants grown in peat/vermiculite mix did reasonably well, as did plants grown in pure peat. The sphagnum is chopped into approximately 3 cm long pieces and lightly packed in the bottom of a 7.5 cm shallow pot to within 2 cm of the top. Then the pot is filled to the top with milled living sphagnum, which I chop in an ordinary food blender. The milled top layer prevents the larger pieces of sphagnum from overgrowing small plants and dormant buds. One plant is planted in each pot except for *P. gypsicola* (four per pot), *P. cyclosecta* (three or four per pot), and *P. parvifolia* (two or three per pot). At this point I would like to add that despite reading several articles written by other growers on adding limestone to their growing medium, my plants were grown without any lime whatsoever. Plants were extremely healthy and prolific, indicating lime is not a necessity for healthy growth.

(Continued on page 51.)



Two forms of *P. moranensis:*
P. moranensis Oaxaca (left)
P. × *kewensis*
Photo by S. Smith

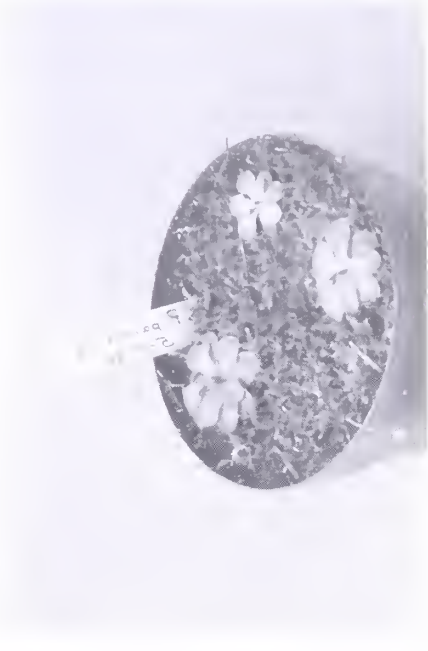


P. cyclosecta

P. lilacina

Photos by S. Smith

P. moranensis



P. parvifolia

Flowers of *D. stolonifera* "Alpine form"

Allen Lowrie looking at colony of *D. stolonifera* "Alpine form" pink flowers.

Habit of *D. stolonifera* "Alpine form"

A FIELD TRIP TO TOOLBRUNUP PEAK*

Allen Lowrie, 6 Glenn Place, Duncraig, 6023, Western Australia

In November 1981, after my friend Robert Oliver had returned from a weekend with his family in the Stirling Ranges (Albany region), he reported to me that on the cliffs of Toolbrunup Peak, at about the 700M mark, he spotted what he thought might be a C.P. in the distance. He didn't really take much notice because the plants were off the main track up the mountain face. After talking about this C.P. possibility, we decided to organise a field trip to Toolbrunup Peak to investigate. I was rather excited at the possibility of finding a new species, since to date no Western Australian C.P. had been discovered at this altitude. (The Stirling Range area has the highest range in the southwest of Western Australia.)

On a Friday night in November 1981, Robert and I set off on the 400 KM drive to the Stirling Range. We arrived about 1:30 a.m. and crashed for the night under the stars. At first light, after breakfast, we set off for the walk up the mountain. The first 300M was okay as it consisted of slowly rising trails; afterwards, however, it was straight up. We were mostly on all fours climbing up and over large rocks, tree stumps and what-have-you. By stopping every 50M or so and resting, we finally arrived at the 700M mark. Walking off the main track to the right and slowly working our way up the cliff face we arrived at the place where Robert had spotted the C.P. Sure enough, they were C.P., but I couldn't identify them immediately. On further investigation, I concluded that they were a form of *D. stolonifera*. There are four basic growth forms of *D. stolonifera* found generally, but this one was a different form altogether, no doubt an alpine form, as in this region snow can be found on Bluff Knoll (1073M). Toolbrunup Peak height is 1052M.

*Albany Region, West Australia

After crawling up the face of Toolbrunup Peak between the 700M mark and the summit, I was lucky enough to find plants in flower. What a surprise to find these *D. stolonifera* "Alpine form" sporting pink flowers! Down on the lower sand plain, *D. stolonifera* is always found with white flowers. The trip up the mountain had certainly produced a new variety of C.P. *D. stolonifera* "Alpine form-Pink flowers" was truly the highlight of all my 1981 field trips. After Robert and I had explored the upper face of Toolbrunup Peak, we called it a day and set off down the mountain. I don't know which was worse—the climb up or the jarred legs on the way down.

Since it was November, the sand plain *D. stolonifera* had finished and were dying back and making up their new tubers, but the *D. stolonifera* "Alpine forms" were just coming into flower on Toolbrunup Peak. Where the *D. stolonifera* "Alpine form" grows is constantly wet, in complete shade all day long, as the plants were found on the South side of the mountain only. The plants were also found mostly growing under rock ledges and in a few cases we found groups of plants in small caves approximately 1M back into the cliff face. Even if the sun did get over to the south side of the mountain, the plants would be in complete shade all day long anyway. This type of C.P. discovery is fairly common here in Western Australia, new varieties are always coming to light anytime one can find a different soil type or different microclimate. Over the years I have only explored the one altitude (the sand plains and hills). The discovery of *D. stolonifera* "Alpine form-Pink flower" at the top of Toolbrunup Peak leads me to believe that the other peaks in the Stirling Range may produce different forms and species of C.P.

Review of Recent Literature

Barrie, N. and M. Honda (photos). 1982. Those blooming meat eaters. National Wildlife 20:40-45.

A popular article on Sarracenias with very brief introductory text, but with six color photos, some two page spread. The photos include the obligatory "view from the pit," of course. Moderately interesting.

Disney, R. H. L., *Megaselia corkerae,* a new species from *Nepenthes* in Hong Kong with reevaluation of the genus *Endonepenthia* (Diptera: *Phoridae*). Orient. Insects 15 (2): 200-206. 1981.

The author found that these insects breed in the pitcher fluid of *N. mirabilis.*

Robertson, A. and B. A. Roberts. 1982. Checklist of the alpine flora of Western Brook Pond and Deer Pond areas, Gros Morne National Park. Rhodora 84:101-115.

Among the plants listed in the diverse habitats of this Newfoundland, Canada coastal montane area are the following CP species: *Sarracenia purpurea, S. purpurea, f. heterophylla, S. purpurea v. venosa* (sic), *Drosera rotundifolia* (incl. a f. *breviscapa*), *D. intermedia, Utricularia minor, U. intermedia* and *Pinguicula vulgaris.* A profile map and brief description of the varying habitats are given. This is a first published location for *S. purpurea* f. *heterophylla* in this area. Note the unlikely and mistaken "v. *venosa*" under *S. purpurea.*

Sibaoka, T. 1980. Action potentials and rapid plant movements. In PLANT GROWTH SUBSTANCES 1979 (F. Skoog, editor), Springer-Verlag, New York. Pp. 462-469.

Mimosa and *Dionaea* are discussed, along with some measurements and comments, with results similar to those presented by Williams, Pickard and others in the past. *Aldrovanda* is new work reported in the paper in which stimuli were applied and sequential measurements made via insertion of microelectrodes. New figures and observations on speeds, direction and extent of action potentials are presented. The mechanism is somewhat similar to *Dionaea* except for numerical differences, and *Adrovanda* usually only requires one sensory hair stimulus to initiate closure.

Sutherst, R. W., et. al. 1982. Tropical legumes of the genus *Sytlosanthes* immobilize and kill cattle ticks. Nature 295:320-321.

While the genus has not been demonstrated to be carnivorous per se, it is of interest that tick larvae, which crawl to the tips of vegetation to await an animal host, are both immobilized in the glandular secretions of some species of this genus, and then killed by an aromatic toxin as demonstrated by partition experiments. This property as well as the nutritious character of this legume may prove of value in animal husbandry.

Whitesell, J. K., Matthews, R. S., Minton, M., & A. M. Helbling. Total Synthesis of Sarracenin. J. Am. Chem. Soc. 103 (12): 3468-3472. 1981.

The authors described the synthesis of the iridoid monoterpene sarracenin from *Sarracenia* species.

Williams, S. E. and B. G. Pickard, 1980. The role of action potentials in the control of capture movements of *Drosera* and *Dionaea.* Springer-Verlag, New York. Pp. 470-480.

This and the paper by Sibaoka reviewed elsewhere in this section were read as part of 10th International Conference on Plant Growth Substances held in Madison, WI, 22-26 July, 1979. This paper is an excellent review of the author's work on action potentials in the genera and is a very useful summary of the several papers published by the authors over the years.

Small *P. gypsicola* cutting

Photo by S. Smith

Orchid Butterworts (Continued from p. 46.)

With the exception of *P. hirtiflora* and *P. lilacina,* these *Pinguicula* form dormant buds during the winter months. Leaves become short, succulent and numerous. These succulent leaves are the best for propagation, and up to ⅔ can be removed from the central bud with no ill effects on next spring's growth.

As with other CP, water must be pure for best results. When and where possible it is best to use rain water. When leaves overlap each other and drape over the side of the pot, care must be taken not to wet the leaves when watering. A large bulb syringe is excellent for watering as the leaves can be carefully lifted and the plant can be watered with a gentle stream.

During the active growing season plants may be fertilized by *lightly* misting with a ⅛ to ¼ strength balanced fertilizer once every four to six weeks. Fish emulsion is not recommended as it entices fungus growth.

These plants can be propagated either sexually or asexually. Thick, succulent winter leaves are spread on milled sphagnum or peat or vermiculite. The medium is lightly moistened and pot placed in a plastic bag that is sealed and placed in a warm, well lit environment. Approximately four to six weeks later small plantlets will begin to grow from the leaf base. When these plants are large enough to work with they are removed and planted in individual pots. Flowers are not self pollinating and pollination must be done by hand. This procedure is the same as for *P. lutea* described in CPN Vol. 8, #2, page 58. Seed pods begin to swell about 10 days after fertilization and mature four to six weeks later. Seeds are spread on milled sphagnum or peat to germinate. Seeds take approximately three to four weeks to germinate.

Those who are interested in obtaining these species should contact W.I.P., P. O. Box 303, Grant, Florida 32949 during the active growing season.

Pinguicula macroceras ssp. *montensis,* growing in Northern California.
Photo by Jurg Steiger.